

THE DENTARY OF *WAKALEO VANDERLEUERI* (THYLACOLEONIDAE: MARSUPIALIA)

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ABSTRACT

A well preserved left dentary of the thylacoleonid *Wakaleo vanderleuerei* Clemens and Plane was recovered from the mid Miocene Camfield Beds (Bullock Creek local fauna) of the Northern Territory, Australia. *W. vanderleuerei* is distinguished from the slightly older *W. oldfieldi* Clemens and Plane by the size of the dentary and morphology of M_2 (= M_1 in Clemens and Plane (1974)), though these differences are not extreme. These features, by analogy with the well represented Pleistocene thylacoleonid *Thylacoleo carnifex* Owen, may be too variable for distinguishing species. The enlargement of P_3 relative to M_2 suggested as a possibly diagnostic character of *W. vanderleuerei* by Clemens and Plane (1974) is confirmed. Additional diagnostic features in the posterior region of the dentary are present in the new specimen and are believed to reflect a refinement in the jaw musculature for a shearing function in the cheek teeth and a modification for an increased gape in the jaws.

KEYWORDS: Miocene, Thylacoleonidae, *Wakaleo*, dentary, functional morphology, taxonomy.

INTRODUCTION

The Thylacoleonidae, with their unusual dentitions, have fascinated palaeontologists since the discovery of *Thylacoleo carnifex* Owen in the 1830's (Finch 1982). The function of the teeth, diet and behaviour of *T. carnifex* were the subject of, at times, vigorous debate in the years following discovery. The various interpretations have been reviewed by Finch (1982) and Wells *et al.* (1982). More detailed studies (e.g. Wells and Nichol (1977), Finch and Freedman (1982), Wells *et al.* (1982), Archer and Dawson (1982)) were not possible until the accumulation of sufficient cranial and post-cranial elements.

Two genera and eight species of thylacoleonids are now recognized (Archer and Dawson 1982). *Thylacoleo* Gervais is known from the Pliocene and Pleistocene, though *T. hilli* Pledge may have occurred in the late Miocene (Pledge 1975), while *Wakaleo* Clemens and Plane is known from the middle and late Miocene. Clemens and Plane (1974) and Archer and Rich (1982) do not consider *Wakaleo* to be directly ancestral to *Thylacoleo* and the phylogenetic relationships of the family are obscure.

Two species of *Wakaleo* are known from the mid Miocene of Australia. *W. vanderleuerei* Clemens and Plane was collected from

the Camfield Beds (Bullock Creek local fauna) of the Northern Territory and *W. oldfieldi* Clemens and Plane was recovered from the slightly older Wipajiri Formation (Kutjamarpu local fauna) of South Australia. *W. vanderleuerei* is thought to be a direct descendant of *W. oldfieldi*. (See Woodburne *et al.* (1985) for a recent review of the continental mammal record of Australia). Both species were described from their incomplete lower dentitions and are distinguished primarily by size of the dentary and morphology of M_2 (= M_1 in Clemens and Plane (1974), Archer (1978)). These differences are not extreme. There are too few data available to demonstrate whether or not the diagnostic characters of the two species overlap due to intraspecific variability.

A well preserved left dentary of *W. vanderleuerei* was recovered from the type locality during the joint Northern Territory Museum/Museum of Victoria field expedition of 1985. The skull of *W. vanderleuerei* recovered from Bullock Creek by M. Plane (description in prep; P.F. Murray pers. comm.) and the dentary fit closely when articulated suggesting the two elements represent the same individual. The M_2 of the new specimen is too worn and poorly preserved to add substantially to our knowledge of this tooth. Clemens and Plane (1974)



LINGUAL



OCCLUSAL



LABIAL

0 50 mm



Fig. 1. Lingual, occlusal and labial views of the dentary of *Wakaleo vanderleueri* (NTM P85553-4).

suggested the absolute enlargement of P_3 and its enlargement relative to M_2 in *W. vanderleuerei* as a possible diagnostic character. The enlargement relative to M_2 is confirmed in the new specimen but it is not certain with so few data whether the absolute size of P_3 differs significantly between the species. Additional diagnostic differences in the posterior region of the dentary are present on the new specimen.

W. alcootaensis Archer and Rich from the late Miocene Waite Formation (Alcoota local fauna) of the Northern Territory is the only other *Wakaleo* described and is known from a maxillary fragment.

Woodburne *et al.* (1985) drew attention to a growing chronologic utility of thylacoleonids but descriptions of few specimens from the Miocene have been published. Accordingly a description of the new fossil is presented here.

Table 1 contains brief descriptions and catalogue numbers of comparable specimens studied by Clemens and Plane (1974). Prefixes to catalogue numbers are as follows: CPC Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra; NTM Northern Territory Museum; SAM South Australian Museum; UCMP Museum of Paleontology, University of California, Berkeley.

DESCRIPTION AND COMPARISONS

The new dentary (NTM P85553-4) was recovered from a limestone block using acetic acid. The teeth and the lingual side of the horizontal ramus lay on the exposed surface of the block and were damaged by weathering (Fig. 1). Alveoli only are present for I_1 and a small single rooted tooth between I_1 and P_3 ; P_3 and M_2 have split vertically along their midline leaving only their labial halves intact; M_3 is undamaged while only the roots of M_4 are present. The buccal side and posterior region of the dentary were protected by limestone. Slight damage to the angular process and the extremity of the coronoid process may be attributed to post-mortem breakage before preservation.

The dentary (excluding the teeth) is described relative to that of *W. oldfieldi* (SAM P17925). The NTM specimen is slightly larger and more robust (Fig. 2). The masseteric fossa is shallower and rather than

having a simple labially concave area of insertion for the deep masseter, the posterior region is flexed lingually, confluent with a deep antecondylar fossa. A small (2 mm diameter) masseteric foramen near the anterior angle of the masseteric fossa has no apparent homologue in a cast of SAM P17925, nor does it appear in Clemens and Plane (1974). The pterygoid fossa is proportionally larger and is partially enclosed in the posterior region by a strut linking the base of the angular process to the base of the condyle. The reinforcement provides a robust base for the strongly inflected angular process. The restored coronoid process sweeps posteriorly to form a relatively deep mandibular notch. The thickened anterior edge of the ascending ramus expresses a slightly convex lateral profile in contrast to the slightly concave anterior coronoid profile of *W. oldfieldi*. The gonial angle of the new specimen (Fig. 2) is greater and consequently the condyle is positioned more posteriorly than that of *W. oldfieldi*. A prominent fossa inferior to the posterior margin of the condyle accommodated the postglenoid process when the jaws were at full gape. This subcondylar fossa is poorly developed in *W. oldfieldi* and its presence in NTM P85553-4 reflects a functional modification in the dentary for an increased gape. The horizontal ramus is deeper and more robust in cross section than *W. oldfieldi*, with a thicker, straighter inferior border and more clearly defined digastric fossa. The post alveolar shelf is terminated posteriorly by a prominent swelling on the lingual side of the coronoid process.

When the skull of *W. vanderleuerei* and the new dentary are articulated it is evident that I_1 must have significantly longer than that of *W. oldfieldi* for the incisors to occlude. The inferred proportions of I_1 are shown in Fig. 2. A plan of the cheek teeth of NTM P85553-4 and measurements are shown in Fig. 3. Comparisons of crown morphology are made difficult by the very advanced stage of wear in the new fossil and the generally poor overlap in material. NTM P85553-4 appears to retain a small alveolus for a single rooted premolar immediately distal to I_1 alveolus. The tooth was probably button-like and protected the gum between I_1 and P_3 . Only the labial half of P_3 is preserved. Two ventrolabially sloping wear facets are pre-

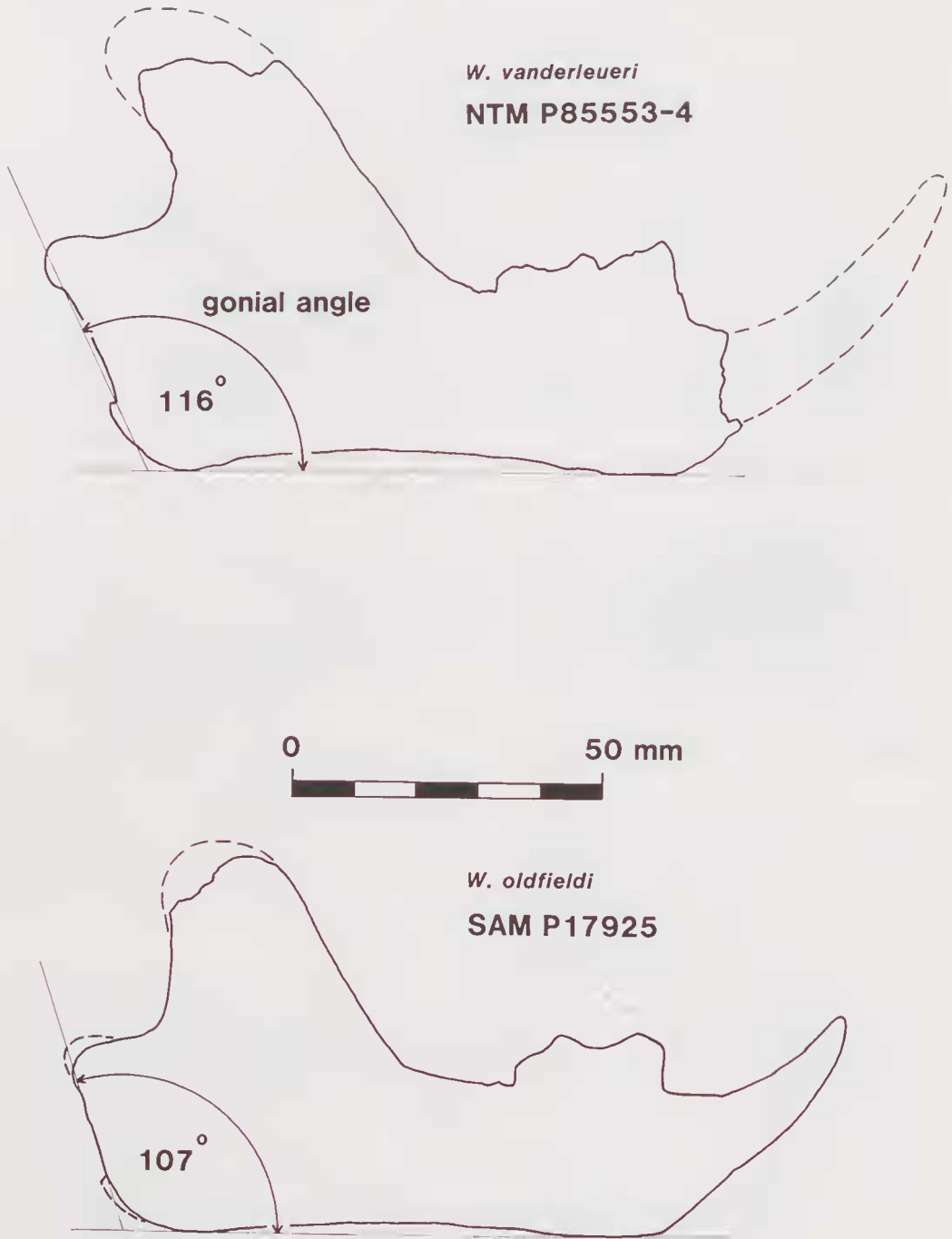


Fig. 2. Partially restored lingual silhouettes of *Wakaleo vanderleueri* (NTM P85553-4) and *W. oldfieldi* (SAM P17925).

sent. The anterior facet, extending from the anterior cusp to a point over the middle of the posterior root, is gently arcuate when viewed from the labial side. Distally a notch-like facet extends posteriorly from the middle of the posterior root across the posterior margin of P_3 and continues onto the anterior portion of M_2 . A single elongated arcuate facet is developed on the P_3 of *W. oldfieldi*. The notch-like facet of NTM P85553-4 accommodated the posterior cusp of P_3 and is probably only present in aged individuals. Apart from age-related wear facet development and proportional differences discussed elsewhere, the P_3 crown morphology does not appear to differ significantly from that of *W. oldfieldi*.

In the NTM specimen the lingual half of M_2 has broken away and tooth wear is far more advanced than in SAM P17925 and CPC 13527. The relative development of the anterior and labial ridges descending from the apical cusp (metaconid) were cited by Clemens and Plane (1974) as diagnostic characters separating *W. oldfieldi* and *W. vanderleuerei*. The M_2 has split on or near the anterior ridge and the labial ridge is completely worn away. Slight irregularities on the labial side of the crown are the only indications that a labial ridge may have been present. The talonid basin is also largely worn away with only a remnant near the posterior margin of the tooth remaining. Four wear facets are present. The anterior one is a continuation of the posterior facet on P_3 . A small concave facet occupies the antero-labial side of the trigonid while the dominant facet extending postero-labially from the apical cusp swings posteriorly across the labial side of the talonid, almost to the posterior margin of the tooth. A small facet bridges M_2 and M_3 . All facets are directed ventro-labially.

The M_3 crown is more worn than UCM P102677. The elevation of the apical cusp has been markedly reduced by wear and there is no sign of an apical basin. The talonid basin is reduced to a small area lingual of the midline of the talonid. As a result of wear, a ridge runs anteroposteriorly across the trigonid close to the lingual margin. It is continued posteriorly by the lingual rim of the talonid basin. Two small cusps are developed on the ridge over the trigonid. A single wear facet is present lingual to the ridge. It plunges postero-lingually from the anterior margin of

the tooth to a point over the anterior edge of the posterior root. The remaining facets slope ventrolabially. One covers the labial slope of the trigonid and three smaller ones cover the talonid. The most posterior facet was probably continued on M_4 .

The overall pattern of facets along the tooth row is reminiscent of a blade from a set of pinking shears. The facets and their contacts comprise a series of ridges and troughs, sub-parallel and sloping ventrolabially. This pattern was probably continued on M_4 , in which case the entire molar row and P_3 were involved in shearing. The tooth row has a marked torsion so that the angle of the facets decreases posteriorly relative to a vertical antero-posterior plane through the dentary. However, the angle relative to the vertical axes of the roots is fairly constant at about 65° .

Comparisons of tooth dimensions are given in Table 2 though proportional differences are clearer in plans of the various tooth rows (Fig. 3). NTM P85553-4 is most likely a smaller individual than CPC 13527, and differs from *W. oldfieldi* in a proportional reduction in the width of the tooth row and the relatively greater length of P_3 .

DISCUSSION

Clemens and Plane (1974) distinguished *W. oldfieldi* and *W. vanderleuerei* by the size of the molars and dentary bones, morphological differences in M_2 and the possible proportional enlargement of P_3 in *W. vanderleuerei*. These differences are not extreme. The geographical separation of the type localities and the apparent difference in age were cited as further justification for the recognition of two species.

The Pleistocene *T. carnifex* is the only thylacoleonid sufficiently represented to allow a statistical analysis of tooth, skull and mandible measurements. Archer and Dawson (1982) found large differences in the size of skulls and mandibles but a uniformity in tooth size. Skull and mandible size was not attributable to allometric changes with increased age of individuals. Finch and Freedman (1982) found no evidence from measurements of P_3 of sexual dimorphism. The morphology of P_3 was one feature used to distinguish the early to middle Pliocene *T. crassidentatus* Bartholomai from *T. carnifex* (Bartholomai 1962). Apparently significant

features on P_3 in small samples of *T. crassidentatus* appear to be variably expressed in large samples of *T. carnifex* (Archer and Dawson 1982). These include the extent of mid-crown thickening, the width of the posterior part of the tooth and the extent of vertical transverse crest development leading away from the main cusp.

If *Thylacoleo* is a valid analogue of *Wakaleo* the diagnostic features used by Clemens and Plane (1974) may be too variable for distinguishing the known mid Miocene species, particularly from isolated teeth. The new dentary has dental measurements that differ in some respects from both the holotypes and referred specimens of *W. oldfieldi* and *W. vanderleueri* and damage to the M_2 and advanced tooth wear preclude the recognition of diagnostic morphological features. It does, however, show a proportional increase in the length of P_3 relative to M_2 . It is not yet possible to determine whether the absolute size of P_3 differs significantly between *W. oldfieldi* and *W. vanderleueri*. Substantial differences in the posterior region of the dentary and the reduced width of M_3 indicate it does not represent *W. oldfieldi* but conspecificity with *W. vanderleueri* is harder to demonstrate. The NTM specimen is assigned to *W. vanderleueri* on the basis of the relative enlargement of P_3 and its recovery from the type locality. There is no clear stratigraphic evidence of a temporal range at the type locality so CPC 13527 and NTM P85553-4 are, geologically speaking, considered contemporaneous. The erection of a new species is not justified.

It is apparent in the new dentary that evolutionary changes from *W. oldfieldi* to *W. vanderleueri* are more marked in the morphology of the posterior region of the dentary than they are in the cheek teeth. The differences in this region may best be explained as a reflection of a refinement in the jaw musculature for a shearing function in the teeth and an anisometric modification to compensate for the probably greater length of I_1 .

Wells *et al.* (1982) found that *T. carnifex* retained essentially phalangerid jaw mechanics in association with a sectorial dentition. In *T. carnifex* the incisors are adapted for stabbing or piercing food and require a simple, though powerful, hinge-like closure of the jaws over a wide range of

angles. The shearing cheek teeth begin to function when the jaws are almost closed. Shearing requires continuous unilateral pressure on the occluding teeth and hence some lateral movement at the hinge and a corresponding medial shift of the mandible. The shearing teeth on one side are thought to have been brought into occlusion by contraction of the deep masseter and the pterygoid complex on the balancing side. Lateral pressure on the shearing teeth may have been provided by a labial longitudinal rotation of the dentary produced by contraction of the superficial pterygoid on the occluding side. This motion requires a flexible symphysis otherwise disarticulation of the balancing dentary would occur. *T. carnifex* has an exceptionally well developed angular process which would provide a substantial base for the insertion of the superficial pterygoid. Wells *et al.* (1982) showed that the shearing blade in *T. carnifex* was positioned within the zone of the maximum bite force of Greaves (1978) for an animal using both occluding and balancing side articulation and musculature for application of the force.

The dentaries of *W. oldfieldi* and *W. vanderleueri* are similar enough to that of *T. carnifex* to indicate a stabbing and shearing function in the teeth.

The robust dentary of *W. vanderleueri* indicates a proportional increase in the masticatory musculature in its evolution from *W. oldfieldi*. The larger angular process and

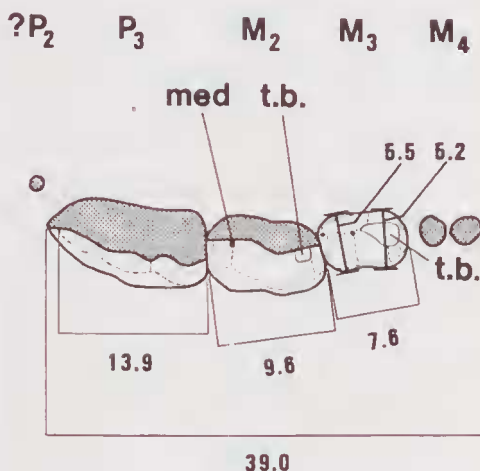


Fig. 3. Plan on the tooth row of NTM P85553-4. Dimensions in mm. Abbreviations: med, metaconid; t.b., talonid basin.

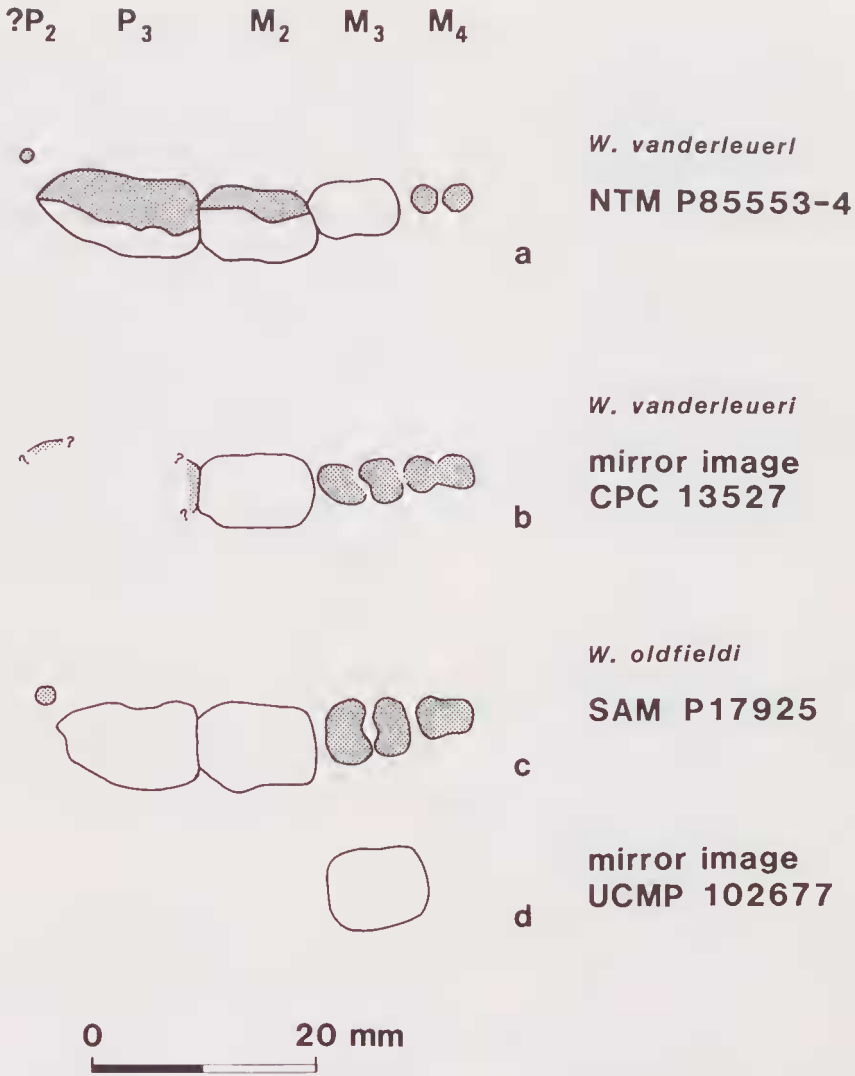


Fig. 4. Comparison of the tooth rows of various specimens of *Wakaleo*: a, prepared from original; b, d, after Clemens and Plane (1974); c, prepared from cast.

modified pterygoid fossa may reflect modification of the pterygoid complex in *W. vanderleueri* for more effective labial rotation of the occluding dentary and medial shift of the mandible during shearing. Additional control may have been provided by insertion of part of the masseter into the ante-condylar fossa. Posterior displacement of the dentary during shearing of a resistant substrate (Wells *et al.* 1982) may also have been resisted by this fibre group, particularly if its line of action had an antero-posterior component.

By articulating the new dentary with the skull of *W. vanderleueri* it is evident that the

incisors could only have occluded if I_1 was significantly longer than that of *W. oldfieldi*. An increased length of I_1 without a compensatory modification for increasing the angle of the jaws at full gape would result in reduced clearance between the upper and lower incisors. In *W. vanderleueri* an increased gape in the jaws has been achieved by an increase in the gonial angle and the development of a subcondylar fossa which accommodated the postglenoid process at full gape. Reduction of the width of the tooth row and relative enlargement of P_3 in *W. vanderleueri* can be interpreted as the evolutionary trend in thylacoleonids for a shearing

function in the teeth derived from a presumed quadritubercular ancestor (Archer and Rich 1982) with grinding molars. Using the geometrical model of Greaves (1978) the area of maximum bite force in *W. oldfieldi* and *W. vanderleuerei* includes both P_3 and M_2 .

Archer and Rich (1982) identify the specialized loss of the two upper and lower anterior premolars as a diagnostic character state for *Wakaleo*. *W. alcootaensis* shows no evidence for P^{1-2} but the available specimens indicate that in the mid Miocene at least, *Wakaleo* retained one of the lower two premolars. The presence or absence of this tooth does not alter the current understanding, as outlined by Archer and Rich (1982), of the phylogenetic separation of *Wakaleo* and *Thylacoleo*.

CONCLUSIONS

Additional diagnostic characters for *W. vanderleuerei* are recognized in the posterior region of the new dentary. They are the presence of a deep antecondylar fossa which is an elaboration of the masseteric fossa; a prominent fossa ventral to the posterior margin of the condyle; reinforcing of the base of the condyle and angular process by a strut resulting in the partial enclosure of the posterior part of the pterygoid fossa. These features are believed to reflect the specialization of the jaw musculature for a shearing function in the teeth and a modification in the dentary to compensate for the inferred greater length of I_1 relative to that of *W. oldfieldi*. Specimens described so far indicate morphological and proportional differences in

Table 1. Comparable material described by Clemens and Plane (1974).

Taxon	Catalogue Number	Description
<i>W. oldfieldi</i>	SAMP17925	Left dentary retaining I_1 , P_3 , M_1 alveoli for M_3 , M_4 and a single rooted tooth between I_1 and P_3 . I_1 , P_3 and M_2 show early stages of wear.
	UCMP 102678	Isolated fragment of anterior half, right P_3 .
	UCMP 102677	Isolated right M_3 showing advanced stages of wear and post-mortem breakage.
<i>W. vanderleuerei</i>	CPC 13527	Right dentary fragment retaining M_2 alveoli for M_3 and M_4 and part of the alveolus of I_1 . M_2 shows only the earliest stages of wear.

Dental terminology follows Archer (1978). M_2 , M_3 and M_4 are referred to as M_1 , M_2 and M_3 respectively in Clemens and Plane (1974).

Table 2. Dental dimensions (in mm) of specimens of *Wakaleo*.

	<i>W. vanderleuerei</i>		<i>W. oldfieldi</i>	
	NTMP85553-4 (After Clemens and Plane 1974)	CPC 13527 (After Clemens and Plane 1974)	SAMP17925 (After Clemens and Plane 1974)	UCMP 102677 (After Clemens and Plane 1974)
P_3 Length	13.9+	13.5-15.3	12.4	
Width (over anterior root)	—	—	6.2	
Width (over posterior root)	—	—	7.8	
M_2 Length	9.6	11.7	10.4	
Width (Trigonid)	—	7.9+	8.7	
Width (Talonid)	—	7.7	7.2	
M_3 Length	7.6			7.5
Width (Trigonid)	5.5			6.3
Width (Talonid)	5.2			6.1
M_{3-4} Total length of alveoli	13.9	14.5	13.7	

the cheek teeth between *W. oldfieldi* and *W. vanderleuri* are subtle. The relative to M_2 enlargement of P_3 in *W. vanderleuri* is confirmed in NTM P85553-4 but it is not yet possible to determine whether the absolute size of P_3 differs significantly between *W. oldfieldi* and *W. vanderleuri*. This was cited as a possibly diagnostic feature by Clemens and Plane (1974). The cheek teeth of *W. vanderleuri* are proportionally narrower than those of *W. oldfieldi*. This follows the evolutionary trend of a shearing specialization in the teeth of thylacoleonids and was derived from a presumed quadritubercular ancestor (Archer and Rich 1982) with grinding molars.

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